THE

AMERICAN JOURNAL OF SCIENCE

[FOURTH SERIES.]

Art. XIV.—*The Ventral Integument of Trilobites;* by C. E. Beecher. (With Plates II–V.)

In previous papers by the writer, on the structure and appendages of *Triarthrus*,[1–5] no attempt has been made to describe or illustrate the character of the ventral integument, especially in the sternal or axial region. The specimens hitherto described were prepared to show details of the appendages, and though portions of the ventral membrane were exposed in many individuals, the subject was not considered of sufficient moment to warrant a distinct study, particularly as no characters were observed in the cuticle that had not been previously seen in more or less perfection by Walcott[10] in the genera *Ceraurus* and *Calymmene*. A recent discovery by Jaekel,[8] however, necessitates the separate consideration of this structure. This necessity arises from the fact that a positive addition to the knowledge of the trilobite anatomy may be deduced, although, as will be shown, Jaekel was apparently entirely misled in his interpretation of the nature of his discovery.

In the paper under discussion, Jaekel[8] states that the occasion for his publication arose from the finding of a specimen of *Ptychoparia striata*, from the Cambrian of Bohemia, in which some structures were preserved in the axis of the six anterior segments of the thorax. These, he asserts, are the proximal joints of the legs.

The specimen was preserved as a cast in a rather coarse-grained sandstone, and is exposed from the dorsal side. From certain surface indications of lines in the cast, Jaekel was led to follow these into the rock filling the axis, and succeeded in

finding a central groove, with two oblique grooves on each side. These he considered as representing the cavities left by the removal of the test from the basal joints of the legs, which thus must have been attached along the median line of the sternum. The supposed joints of the legs were filled with rock, and his attempts to separate them from the matrix resulted in failure.

In the oral region, there were still more indefinite and obscure evidences of cavities left by the removal of some ventral testaceous structure.

These meager remains in the rachis of the thoracic and oral regions have furnished data for what must be considered as the most remarkable and erroneous reconstruction of the trilobite appendages and anatomy that has appeared since the time of Burmeister,[7] in 1843. The latter, in the absence of any material, confessedly based his opinions of the ventral anatomy wholly upon theoretical considerations. Not only has Jaekel to a large degree set aside the evidence presented by many scores of specimens of *Triarthrus*, as described by the writer, in which each detail of structure can be verified indefinitely, but has also overlooked that afforded by the material illustrated by Walcott,[10] Billings,[6] Mickleborough,[9] and Woodward.[12] Moreover, this single specimen of *Ptychoparia* has led its describer to reconsider on a false premise the entire question of the anatomy, ontogeny, phylogeny, and affinities of the trilobite.

It is the purpose of the present article to show that numerous individuals of *Triarthrus*, as well as some material representing other genera, preserve evidence of what seems to be the same structures as those described by Jaekel in *Ptychoparia*, and also present indisputable testimony as to their correct nature. It will be demonstrated that they do not belong in any way to the appendicular system of the trilobites, but are really the buttresses and apodemes of the ventral body integument.

The marvelous state of preservation of many of the specimens of *Triarthrus*, whose appendages have been studied by the writer, affords very satisfactory indications, not only of the presence of a ventral integument, but also of some of its detailed characters. Jaekel states that in his opinion the *unfavorable* ("*ungünstigen*") preservation of *Triarthrus* has obscured the proximal structure of the legs, so that what he calls the three basal joints are equivalent to the single unjointed gnathobase of the coxopodite, as described by the writer. Inasmuch as Jaekel has never seen the original specimens described, his statement is practically without foundation. It may also be added that the types and best-preserved individuals have been

retained in the collections of the Yale University Museum. The photographic illustrations accompanying this article, it is believed, will refute his statement, and the specimens themselves would serve the same purpose more completely, since from the black nature of the rock and the nonactinic character of the fossils the photographs feebly represent the delicate structures actually preserved, which are clearly visible to the eye.

The ventral membrane of *Triarthrus*, as well as of other trilobites where it has been observed, is of extreme tenuity and only under the most favorable conditions has it been preserved. The membrane itself was a thin, uncalcified, chitinous, flexible pellicle, and thus was in strong contrast with the much thicker and calcified dorsal test.

In the preparation of a specimen to show the appendages from the ventral side, very little of the ventral membrane is commonly exposed, owing to the crowded arrangement of the legs, but when the appendages are removed it is possible to view the entire ventral integument. This process has been carried out in a considerable number of specimens, and some of the more evident characters are herewith described.

The membrane under each pleuron (pleurotergite, Jaekel), or the pleurosternite, as it may be termed,* was smooth and extremely thin, and in the fossils it is invariably concave. This was probably the condition during life, to allow space for the biramous legs and for their infolding during enrollment. It should be noted, however, that the dorsal and ventral integuments in the fossils are generally very close together throughout, leaving but a small cavity for the soft parts of the animal. The space inside has doubtless been considerably reduced by partial collapse from the decay of the soft parts of the animal and also by the pressure of the sediments. The size of the body cavity is unquestionably more correctly shown in the specimens described by Walcott[10] and Mickleborough,[9] from the Trenton limestone and Cincinnati shales, respectively, where they have apparently suffered less compression.

Walcott showed that the membrane in *Calymmene* and *Ceraurus* was strengthened in each segment by a transverse arch, to which the appendages were attached at the sides of the axis. These arches were connected by a thinner membrane

* Jaekel has suggested the name mesotergite to supplant the terms axis or tergum, and pleurotergite in place of pleuron or epimerum, as applied to the trilobites. This seems a useful terminology since the older terms are often loosely used and have somewhat different meanings in other groups. Applying this system of nomenclature to the ventral integument, the writer would propose the terms *mesosternite* for the membrane beneath each mesotergite, and *pleurosternite* for the membrane beneath each pleurotergite. The interarticular membranes are not included.

(the interarticular membrane), and were aptly compared to the arches in the ventral integument of many of the decapods. Similar features are present in *Triarthrus*, as illustrated in Plate IV, figure 1, and Plate V, figures 2–4, where it is seen that the interarticular membrane (Plate V, fig. 4) in a normally extended individual is somewhat less than half the length of the arches. The chitinous integument of the arches, or mesosternites, as they may conveniently be called, is thickened along the borders, and appears to be slightly incurved on the posterior edge. The arches are further strengthened by a series of median and oblique longitudinal ridges, or buttresses, which are generally progressively more developed in passing anteriorly from the pygidium along the thorax to the neck segment of the cephalon.

The ventral arch of each segment has the following arrangement of these ridges: There is first a median ridge generally extending from the posterior border entirely across the plate, but sometimes becoming obsolescent near the anterior border. Then, on each side, there is an oblique ridge making an angle of about sixty degrees with the posterior edge and extending inward, but not meeting, the median ridge, thus enclosing a subtriangular space with the anterior apex truncated. Outside of these ridges but still within the axial region there is often a second pair of somewhat more oblique ridges, enclosing rhombic areas.

The ridges are clearly produced by a thickening of the ventral integument, and can be seen when viewed from the dorsal side of a specimen in which the dorsal test and filling of the body cavity have been removed. *They are thus partly or wholly of the nature of apodemes, or plates of chitin, which pass inward from the mesosternites and divide as well as support internal organs, and they are not, therefore, in any sense the proximal joints of legs.* Besides serving in this manner they were doubtless efficient in giving the necessary firmness to the ventral arches for the attachment of muscles.

Were these observations confined wholly to the specimens of *Triarthrus*, there might still be some chance of error, although it is believed that the evidence presented by this genus alone is quite sufficient. Additional data, however, will now be given, regarding other genera and families of trilobites, described independently by other authors, and with no intention of representing the detailed characters of the ventral arches. In the search for trilobite appendages by various investigators, the ventral membrane has naturally been of secondary consideration, and in the case of Jaekel's work was of no consideration whatever.

The earliest studies and illustrations of trilobites giving some evidence of the nature of the ventral membrane are those by Walcott on the genera *Calymmene* and *Ceraurus*. The limitations of the ventral body walls of the animal were clearly shown by a marked change in the color of the rock between the white calcite filling the body cavity and the dark limestone matrix. In figure 7, Plate V, after Walcott,[10] showing a transverse section of *Calymmene* in the thoracic region, it is seen that the membrane in the axis, or the mesosternite, is marked by four distinct lobes representing cross sections of longitudinal folds, and also that the legs are clearly attached at the sides. These folds can in no way be construed as proximal joints of legs. The gnathobases in *Calymmene* are given in sections, in figure 3, Plate III, of Walcott's paper, and of *Ceraurus*, in figure 2 of the same plate. During a recent visit at the Museum of Comparative Zoology, the writer examined many of the sections made by Walcott during his long and successful search for trilobite appendages. The structure shown in the figure here given (Plate V, fig. 7) was verified, and other sections were observed in which the folds were more pronounced, sometimes extending as thin laminæ into the body cavity, thus having the character of a normal apodeme.

The second instance to be noted, where the ventral membrane has previously been illustrated, is a specimen of *Asaphus megistus* Locke, first described by Mickleborough[9] from the Cincinnati shales in Ohio. In his figure, an outline of which is here reproduced (Plate V, fig. 5), there are shown a number of discontinuous longitudinal lines in the axis of the posterior thoracic region. Mr. Charles Schuchert has kindly examined the original specimen, now preserved in the United States National Museum, and writes that the longitudinal wrinkles in the axis are organic and not due to accident nor to tool marks. In the best-preserved series "there are five longitudinal ridges, a central one with two on each side." They appear in cross section as shown in the sketch furnished by Mr. Schuchert (Plate V, fig. 6).

The correct interpretation of this specimen, as illustrated by Mickleborough[9] and Walcott,[11] is: That the club-shaped bodies lying within the axis are the gnathobases attached at the sides of the axis; the curved members extending outward from the gnathobases are the endopodites; the longitudinal ridges in the ventral membrane between the inner ends of the gnathobases are the buttresses and apodemes of the mesosternites; the slender oblique rod-like bodies shown in the right pleural region in Walcott's figure are portions of the fringes of the exopodites.

The last specimen to be noted in this connection is the individual of *Ptychoparia striata*, already mentioned as described by Jaekel.[8] A reduced photographic reproduction of his figure (Plate V, fig. 1) is presented here for comparison with similar structures, as described in *Triarthrus*, *Calymmene*, *Ceraurus*, and *Asaphus*. From the data here deduced, it would seem obvious that the specimen shows the imprint of the ventral integument in the axial region, the dorsal test and filling of the body cavity having been removed. As in *Triarthrus*, the body has suffered collapse, thus bringing the dorsal and ventral walls quite near together. In the middle of each of the five or six anterior ventral arches is a groove left by the solution of the chitinous median apodeme, or buttress. On either side are two oblique grooves limiting two subangular areas, and outside of these are two other oblique grooves marking off subrhombic areas. The grooves in each case represent the cavities left by the removal of the chitinous thickenings of the membrane of the trilobite. Jaekel's attempt to remove the rock filling these areas naturally was ineffectual, since the latter represent the actual impression of the ventral integument. Were they simply the fillings of the hollow leg joints, as he claims, they should be readily detached from the matrix.

The foregoing descriptions and discussions of the character of the ventral integument in trilobites would have little or no scientific value, and would be about as useless as a minute analysis of the nodes and tubercles on the glabella of a *Phacops*, were it not for the fact that from them it is possible to reach some conclusions regarding the musculature of trilobites, and thus add something to the knowledge of their internal organization.

In the abdomen of a normal crustacean, as is well known, there is a pair of longitudinal dorsal muscles, the *extensors* of the abdomen. They divide into bundles, which are attached on the inner surfaces of the tergites of the somites. Likewise, on the ventral side, there is a larger pair of longitudinal muscles, the *flexors* of the abdomen, from which strands are given off and attached to each sternal arch. The strands from one somite unite with the main bundles within the cavity of the next anterior somite. In a diagrammatic form, this disposition of the ventral muscles is represented in the accompanying figure (fig. 1).

Now, since in crustacea it is of very common occurrence to have chitinous extensions of the integument within the body cavity either to divide or to support organs, as well as for the attachment of muscles, it seems a necessary conclusion to refer the thickenings and buttresses on the ventral membrane of trilobites to the same class of structures, which are usually

termed apodemes. With this interpretation, the median longitudinal ridge on the mesosternite of a trilobite would indicate the line of division between the two main ventral bundles. The first pair of oblique ridges on each side would delimit the main bundles and side strands, and show that these strands joined the main bundles obliquely within the cavity of the next anterior somite, as in ordinary crustacea. This accounts for the anterior truncation of the triangular area between the median and lateral ridges in the trilobite.

The nature of the outside pair of oblique ridges is not so plain. They may serve to divide the side ventral strands of the flexors from the bundle of muscles running from the proximal joints of the legs to the dorsal test, or they may simply mark the outside of the lateral strands.

1

FIGURE 1.—Diagram of the axial portions of three segments; showing the ventral abdominal muscles, the flexors, represented as two heavy longitudinal lines, together with the lateral strands attached to the sternal plate in each somite and continuing obliquely forward to their union with the main bundle in the cavity of the next anterior somite.

The apodemes in general seem more strongly developed anteriorly in the thorax. Possibly, this condition may be explained on the basis that the ventral pair of the great flexor muscles received new strands at each segment from behind forward, so that near the cephalon they became large bundles for which progressively larger apodemes were formed.

It may be remarked, in conclusion, that a similar though apparently much simpler apodemal arrangement would be developed if the musculature of the trilobites agreed with that of the theoretical crustacean ancestor, or that existing in some Isopods, Amphipods, etc., in which there are no large longitudinal bundles, but motion between the somites is effected by strands running from one segment to the next anterior. If viewed in this manner, there would necessarily be two median and two lateral strands. The previous explanation seems to be more in accordance with the structures actually seen in the trilobites, which in general possessed the power of enrollment to a high degree, and would be expected to have had a well-developed and efficient system of ventral muscles.

Summary.—The ventral integument in trilobites is a thin uncalcified membrane, which may be divided into pleurosternites and mesosternites, corresponding to the mesotergites and pleurotergites of the dorsal test, and like them connected segmentally by an interarticular membrane.

The mesosternites are usually marked by five longitudinal ridges, or buttresses, representing thickenings of the membrane, which may be homologized with apodemal structures in other crustacea, and not with the appendicular system.

These buttresses, or apodemes, include a single median one for each mesosternite, with two others on each side extending forward and obliquely inward, and enclosing subtriangular or rhombic spaces.

The presence and disposition of these buttresses apparently afford information regarding the ventral musculature of the trilobites. A pair of flexors is indicated, together with the lateral strands attached to each mesosternite and extending forward and inward to their union with the main bundles within the cavity of the next anterior somite.

Yale University Museum, New Haven, Conn., January 24th, 1902.

References.

1. Beecher, C. E.—On the thoracic legs of Trilobites. This Journal (3), vol. xlvi, 1893.

2. ———.—On the mode of occurrence, and the structure and development of *Triarthrus Becki*. American Geologist, vol. xiii, 1894.

3. ———.—The appendages of the pygidium of *Triarthrus*. This Journal (3), vol. xlvii, 1894.

4. ———.—Further observations on the ventral structure of *Triarthrus*. American Geologist, vol. xv, 1895.

5. ———.—The morphology of *Triarthrus*. This Journal (4), vol. i, 1896; Geological Magazine, dec. iv, vol. iii, 1896.

6. Billings, E.—Notes on some specimens of Lower Silurian Trilobites. Quarterly Journal of the Geol. Soc., London, vol. xxvi, 1870.

7. Burmeister, Hermann:—Die Organisation der Trilobiten, etc. 1843.

8. Jaekel, Otto.—Beiträge zur Beurtheilung der Trilobiten. Theil I. Zeitschr. der Deutschen Geolog. Gesellschaft, Bd. liii, Heft 1, 1901.

9. Mickleborough, J.—Locomotory Appendages of Trilobites. Jour. Cinti. Soc. Nat. Hist., vol. vi, No. 3, 1883.

10. Walcott, C. D.—The Trilobite: New and Old Evidence relating to its Organization. Bulletin Mus. Comp. Zool., vol. viii, No. 10, 1881.

11. ———.—Appendages of the Trilobite. Science, vol. iii, No. 57, 1884.

12. Woodward, Henry.—Note on the Palpus and other Appendages of *Asaphus*, from the Trenton Limestone, in the British Museum. Quarterly Journal of the Geol. Soc., London, vol. xxvi, 1870.

EXPLANATION OF PLATES.

Plate II.

Triarthrus Becki Green.

Figure 1.—A specimen viewed from the dorsal side; showing the extent of the antennules and the limbs on the right side. Enlarged about three diameters.

Figure 2.—The ventral side of a pygidium; showing at the left of the median line the form and disposition of the exopodites and endopodites. The conical ends of the joints of the endopodites are provided with bundles of stiff hairs. Owing to the concavity of the specimen, it is impossible to show it all in proper focus. Enlarged ten diameters.

Figure 3.—The posterior portion of an individual viewed from the ventral side; showing the distal ends of the exopodites, with their setæ and long fringes. Enlarged nearly ten diameters.

Figure 4.—Dorsal view of an individual; showing the nine pairs of anterior thoracic limbs fully extended on the left side. The jointed endopodites and fringed exopodites may be clearly differentiated. Enlarged about three diameters.

Figure 5.—A still further enlargement of some of the limbs of the preceding specimen; showing in more detail the distinctive characters and arrangement of the exopodites and endopodites. Enlarged about ten diameters.

Utica slate, Ordovician, near Rome, New York.

This plate of illustrations, although very inadequately representing the actual objects, is introduced mainly to show the exquisite character of preservation of the specimens of *Triarthrus*.

Plate III.

Triarthrus Becki Green.

Figure 1.—Ventral view of an individual; showing the basal joints of the antennules, the biramous appendages, and the series of gnathobases. The appendages within the cephalon indicate their biramous structure like those over the thorax. They are therefore not simple as restored by Jaekel. The anal opening is shown near the extremity of the pygidium, but is obscure on account of not being in focus. Enlarged three and one-half diameters. (Original of figure 1, Plate IV, vol. xv, American Geologist, 1895.)

Utica slate, Ordovician, near Rome, New York.

Plate IV.

Triarthrus Becki Green.

Figure 1.—The ventral side of an individual prepared to show the character of the endopodites of the entire thoracic series. The gnathobases are distinctly seen extending obliquely inward from the sides of the axis; then follow, within the pleurosternal region, the subtriangular joints of the endopodites with more slender distal joints. The origin and course of the antennules at the sides of the hypostoma are also shown. In the middle of the axis of the mid-thoracic region, the ventral membrane is exposed, and the transverse limitations of the sternal arches and interarticular membrane may be observed. The arches show the buttresses or ridges of apodemal nature, as described in the text. Enlarged three and one-half diameters.

Utica slate, Ordovician, near Rome, New York.

PLATE V.

FIGURE 1.—*Ptychoparia striata* Emmr. *Dorsal* view of the anterior portion of a specimen preserved as a cast in sandstone, and enlarged about two diameters. In the glabellar and anterior thoracic region, the filling of the body cavity has been removed from the axial region, thus exposing the imprint of the hypostoma and ventral integument with its buttresses, or apodemal structures. Reduced from the original figure published by Jaekel. Cambrian, Bohemia.

FIGURE 2.—A specimen of *Triarthrus Becki* Green; viewed from the *ventral* side. The appendages have been removed and the ventral membrane exposed. In the glabellar region are seen the hypostoma and just below it the semicircular convex metastoma with side lappets. Below, in the axial region, the buttresses and thickenings of the sternal arches are clearly marked, as described in the text. Enlarged about nine diameters.

FIGURE 3.—The same specimen enlarged only a little more than three diameters. The illumination is from the side opposite to that in the preceding figure.

FIGURE 4.—*Triarthrus Becki* Green. The ventral side of the middle thoracic region of the specimen illustrated on Plate IV; showing the ends of the pleurotergites on the outside, with the joints of the endopodites within the pleural regions, and the gnathobases extending obliquely inward in the axis. The sternal arches with their longitudinal ridges and the interarticular membranes are represented. Enlarged four and one-fourth diameters. The extensions of the limbs beyond the carapace are omitted.

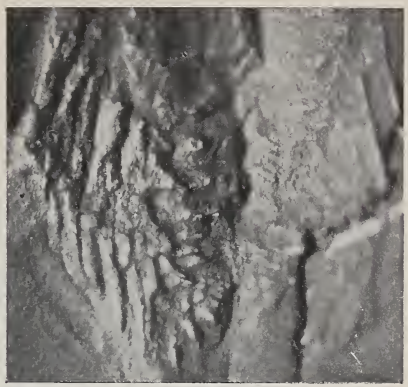
FIGURE 5.—*Asaphus megistus* Locke. A reduced outline of the figure published by Mickleborough;[9] showing the endopodites in the pleural areas, with the gnathobases extending obliquely inward from the sides of the axis, and in the posterior thoracic median line the ridges or folds of the ventral integument. One-half natural size.

FIGURE 6.—An enlarged profile of the mesosternal ridges of the preceding; from a sketch furnished the writer by Schuchert. The lower represents the ventral aspect.

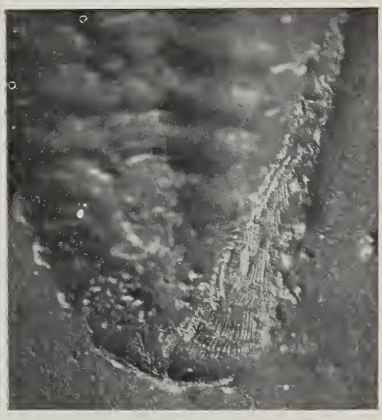
FIGURE 7.—Transverse section through the thoracic region of *Calymmene senaria* Conrad; after Walcott; to show the folds of the ventral integument and the basal joints of the legs, with their points of attachment at the sides of the sternal arch. Enlarged three diameters.

1

2



3



4

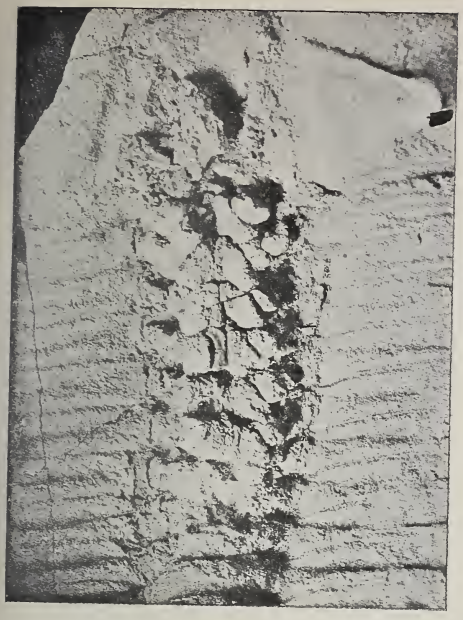
5

Appendages of Triarthrus.

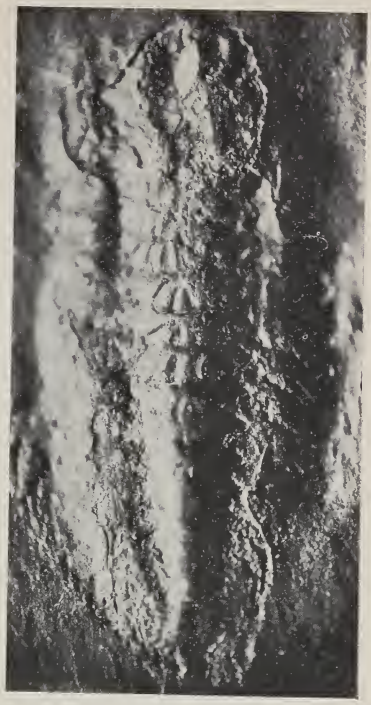
1

Ventral side of Triarthrus.

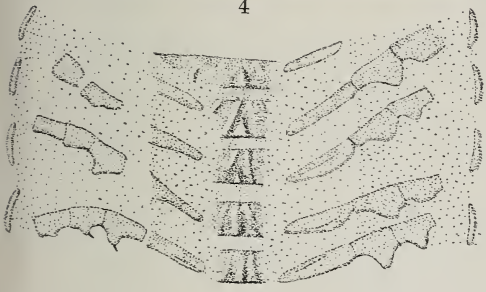
1



2

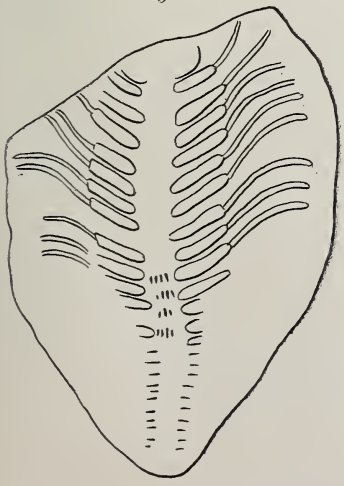


4



3

5



6

7

Ventral integument of Trilobites.